# VESICULAR-ARBUSCULAR MYCORRHIZAE FROM SAGEBRUSH STEPPE HABITAT IN WESTERN IDAHO AND PARTS OF EASTERN AND CENTRAL OREGON

by

M.C. Wicklow-Howard Boise State University Boise, Idaho

Prepared for:
Eastside Ecosystem Management Project

November 1994

# INTRODUCTION

Vegetation dominated by species of sagebrush (Artemisia L.) occupies a substantial portion of the 11 western states, with the bulk of the distribution in Utah, Nevada, southern Idaho, eastern Oregon, western Montana, Wyoming, and Colorado (Blaisdell et al. 1982). This vegetation type is generally characterized as sagebrush steppe (Barbour et al, 1987). Vegetation is dominated by species and subspecies of sagebrush. Other associated shrub species can include: rabbit brush (Chrysothamnus nauseosus (Pursh) Britton), greasewood (Sarcobatus vermiculatus (Hook.) Torr.), saltbush (Atriplex (Tourn) L.). Native bunchgrasses in the sagebrush ecosystem include species of Festuca, Poa, Agropyron, Sitanion, Oryzopsis, and Stipa. Occasional herbaceous perennials occupy sites within these sagebrush/bunchgrass complexes.

Some areas of sagebrush steppe habitat has been converted to farmland, while other areas have been degraded by livestock overgrazing and repeated fires. This has resulted in reduced shrub and native bunchgrass cover and invasion by exotic annual grasses such as Bromus tectorum and Taeniatherum caputmedusae (West 1988). Insouthwestern Idaho, the conversion of the Sagebrush steppe to annual grassland has resulted in increased fire frequency to intervals of less than 5 years.

The sagebrush steppe of southwestern Idaho and eastern

Oregon extends from elevations of approximately 2000 ft (610 m) to about 9500 ft (2896 m). Annual precipitation would be less than 20 inches per year, and would come mostly in the form of winter snow and spring rain, mostly in the months of May and . June.

The sagebrush steppe habitat of southwestern Idaho and eastern Oregon are represented by a range of soil conditions. This variability in the soils reflects the diversity in topography and parent materials found in the areas. The wide valley floors of the basin and Range Province of the Snake River Plain have soils classified as Calcixerolls, Argixerolls, and Calciorthids. In eastern Oregon, these regions of Basin and Range Province have soils classified as Haplargids, Durargids, and Vitandepts. The High Lava Plains-Province as found in parts of Central Oregon has soils classified as Haplargids, Camborthids, and Vitandepts.

### VESICULAR-ARBUSCULAR MYCORRHIZAE

The term mycorrhizae defines a structural as well as functional association: A mycorrhizae is a mutualistic symbiosis between plant and fungus localized in a root in which energy (carbon compounds) move primarily from plant to fungus and inorganic resources (principally phosphate) move from fungus to plant.

One type of mycorrhizae is termed an endomycorrhizae. In endomycorrhizae, following hyphal penetration into the root, the hyphae penetrate the cell walls of the corticle cells. These types are generally called vesicular-arbuscular mycorrhizae (VAM). The intracellular hyphae produce structures that frequently branch many times within the host cells. These structures are known as arbuscules. Arbuscules are the organs where nutrients and carbon are exchanged between host and fungus. Typically, also formed are vesicles, which are fungal storage units. The hyphae within the cells and older roots are subsequently reabsorbed by the host. The association is specifically referred to as a vesicular-arbuscular mycorrhizae (VAM). VAM are found in nearly all families of angiosperms and in some ferns, mosses, and liverworts.

Vesicular-arbuscular mycorrhizal (VAM) associations are found in a broad range of habitats, including the semi-arid grasslands. Not only are these associations geographically widespread, but

within most communities surveyed, mycorrhizae are abundant both within individual root systems and among the array of plant species present. For example, in semi-arid grassland, 95% of the dominant plant species have mycorrhizae, and as much as 96% of the root length can be colonized (Davidson & Christensen, 1977).

VAM fungal reproductive structures are in the form of external spores, which are formed either singly or in small masses. These spores, plus hyphal fragments, and root segments represent propagules which can be dispersed and utilized as inoculum for new host plant colonization. The primary vectors for dispersal of mycorrhizal inoculum are wind and animals. VA mycorrhizal fungi have been demonstrated to be wind-blown up to 2 km (Warner et al., 1987). A wide range of animals are known to disperse mycorrhizal fungal propagules, and generally, any animals that moves soil can cause the migration of mycorrhizal fungi. Of particular interest in shrub deserts are harvester ants, where they will concentrate mycorrhizal inoculum by lining their seed chambers and tunnels with roots containing a high density of mycorrhizal fungi (Friese and Allen, 1988).

It is well established that most of the plants characteristic of shrub steppe habitat are associated with vesicular-arbuscular mycorrhizal fungi (endomycorrhizal fungi). VAM associations are widespread among plant families and very few families are non mycotrophic. Hence, in sagebrush steppe plants belonging to the Asteraceae, Poaceae, and Rosaceae are usually mycorrhizal.

mycotrophy appears to be restricted to families such as the Chenocodiaceae, Brassicaceae, Amaranthaceae, 'and Zvgophvllaceae
(Trappe, 1981). However, within these non-mycotrophic families, it has been reported that in arid ecosystems species of these plants will become mycorrhizal.

VAM fungi involved are species of the Endogonaceae (Zygomycetes) (Gerdemann and Trappe, 1974). Only three genera of VAM fungi are known to form associations with plants in the shrub-steppe habitat of southwestern Idaho and eastern Oregon. These genera are: Glomus Tul. & C. Tul., Gigaspora Gerdemann & Trappe, and Acaulospora Gerdemann & Trappe.

# VESICULAR-ARBUSCULAR MYCORRHIZAE FROM SAGEBRUSH-STEPPE HABITAT OF WESTERN IDAHO AND PARTS OF CENTRAL AND EASTERN OREGON

Table 1. lists the important shrub species of the southern Columbia Basin that have been reported to form VAM. The species of plants are listed by family. Few reports exist on species of VAM fungi associated with arid land shrubs in the southwestern Idaho/southeastern Oregon region of the Columbia Basin. Reports on the shrub species of this region have come from Gurr and Wicklow-Howard, 1994; Rose, 1980; Rose and Trappe, 19'80; Wicklow-Howard, 1982; Wicklow-Howard, 1985.

For each species of plant, the general site within southwestern Idaho and eastern Oregon is given. If the VAM fungus was identified in the report, the fungus name is given. Several plants are identified as being VAM, but the fungal species is not known.

The species, although limited in number, appear to be widespread within their specific habitats. The central Oregon species, associated with plants growing in volcanic ash and sand soils are somewhat similar throughout the site. Glomus gerdemannii has been reported only in these pumice soils in Oregon associated with Ceanothus velutinus and Pursia tridentata (Rose, Daniels and Trappee, 1979). This may be an example of a single species being restricted to specific shrubs.

When compared to species from the lower elevations, drier climate, the species are seen to be different. In southwestern Idaho sites, *Glomus microcarpus* appears to be a dominant species. Other VAM species remain undetermined.

Studies on vesicular-arbuscular mycorrhizal associations of shrub and shrub-like plants of arid and semiarid lands worldwide show the same three genera of VAM fungi. A listing of the shrub species and their associated VAM fungi are presented by Lindsey (1984).Included in this list are sagebrush dominated sites in Wyoming and Colorado. Although the listing includes a wide variety of shrub species which demonstrate VAM colonization, few of these studies have identified the species of fungus involved. Studies of Artemisia tridentata from sites in New Mexico, identify a number of VAM fungal species, including Glomus fasciculatum, Glomus macrocarpum, Glomus microcarpum, Glomus mosseae, Gigaspora margarita, Glomus sp., Acaulospora sp., and Gigaspora sp. (Lindsey, 1984). Bethlenfalvay et al (1985) reported mycorrhizal colonization for a big sagebrush (Artemisia tridentata spp. Wyomingensis) grassland community in Central Nevada. Glomus mosseae (Nicol. & Gerd.) Gerd & Trappe and Glomus constrictum Trappe were isolated. On sites in semiarid range in Northern Nevada, Bethlenfalvay and Dakessian (1984) reported on the presence of Glomus fasiculatum (Thaxt. sensu Gerd.) and Glomus clarum Nichol. & Schenck. There is need for further work on the shrubs and their associated VAM species within the Columbia Basin assessment area.

Table 2 is a list of reported vesicular-arbuscular mycorrhizal associations of perennial grasses and forbs from sagebrush steppe habitats in western Idaho and parts of eastern and central Oregon. The list includes plant species, collection site, and VAM fungus, if known. Reports on vesicular-arbuscular mycorrhizae of perennial grasses and forbs in the Columbia Basin assessment come from the following sources: Maser, Maser, and Molina (1988); Molina, Trappe, and Strickler (1978); Trappe, (1981); Wicklow-Howard, (1982). Wicklow-Howard, (1982).

Molina and Trappe (1978) studied the mycorrhizal fungi associated with Festuca in the western United States and Canada. Plants were collected from grassland communities within eight states west of the Continental Divide and included four sites within the Columbia Basin assessment. This report on the genus Festuca is the most complete examination available of vesicular-arbuscular mycorrhizal colonization of plants and the associated mycorrhizal fungi for the assessment area. Studies from southwestern Idaho sites identify the mycotrophic plants, however the associated VAM species remain unknown.

#### FUNCTIONAL ROLE OF MYCORRHIZAE

Two different types of extramatrical hyphae are produced by VAM fungi: runner hyphae and absorbing hyphae. Runner hyphae are thick-walled hyphae that track roots into the soil. The hyphae that penetrate roots are initiated from runner hyphae. An underground network of interconnecting runner hyphae can form between plants of the same species or different species. VAM runner hyphae will be found in the interspace regions typical of sagebrush-grasslands. The absorbing hyphae form a dichotomously branching hyphal network extending into the soil from the runner hyphae. These hyphae appear to be the portions of the fungus that absorbs nutrients from the soil for transport to the host (Allen, 1991). The fungal hyphae extending into the soil serves as an extension of the root systems; extensions that are both physiologically and geometrically more effective for nutrient absorption than the roots themselves (Read, 1984; Read et al., 1985).

Mycorrhizal root systems are of benefit to their respective hosts by increasing the capacity of the roots to absorb nutrients from the soil (Marks and Kozlowski, 1973). This is apparently accomplished in several ways: (1) the root-absorbing surface is markedly increased (measurements have indicated that in some instances total root surface was increased 30 times more than an uninfected root); (2) hyphae radiating from the mycorrhizal root is able to penetrate farther into soil than the root hairs of

non-mycorrhizal roots; (3) more phosphate (P) uptake per unit area of mycorrhizal roots than nonmycorrhizal roots.

Mycorrhizae have long been known to affect the P nutrition of host plants, as well as have the ability to absorb other mineral nutrients. Phosphate, the major form of P available for uptake by plants, is relatively insoluble in the soil solution and, therefore, is not readily transported by mass flow. Thus, as mycorrhizal hyphae explore the bulk soil beyond the root hairs, additional P is taken up by the hyphae and transported to the host. Mycorrhizal hyphae, by growing into the soil matrix, can gain access to bulk soil P beyond the depletion zones created by the plant roots (Allen, 1991). Soil P concentrations under the shrub Artemisia tridentata increased with time in a successional shrub desert but declined in the associated interspace regions occupied by mycorrhizae. Hence, mycorrhizae may be involved in the development of these "islands of fertility" that characterize arid regions. (M. Allen, 1988; Skujins and Allen, 1986).

The major limiting factor for both nutrient uptake and productivity is drought. VAM infection has been shown to increase water uptake and to increase drought tolerance of several plant species. A suggested mechanism for enhanced water uptake is that it is P mediated, i.e. increased uptake of phosphate by plants results in an increased water uptake and transpiration (Safir and Nelsen 1985). Allen and Boosalis (1983) demonstrated that two different VAM species (Glomus fasciculatum

and <u>G. mosseae</u>) affected the water relations of wheat (<u>Triticum aestivum</u>) differently. <u>G. fasiciculatum</u> improved the drought tolerance of wheat and <u>G. mosseae</u> reduced drought tolerance of wheat..

Trent, Svejcar, and Blank (1994) working in sites northwest of Reno, Nevada quantified VAM arbuscular root colonization, hyphal root colonization, and mycorrhizal hyphal length through the plant growing season for 2 years in Artemisia tridentata ssp. tridentata and Artemisia tridentata ssp. vaseyana. In this study the relationship of these parameters to changes in both soil moisture and temperature is made. Mycorrhizal activity was greater for the subspecies that received slightly more precipitation and occupied a site lower in available nutrients. Arbuscule production and hyphal lengths appeared to be most closely associated with soil moisture and thus plant activity.

Nitrogen and phosphorus are most abundant in upper soil horizons (West, 1991), and their availability to plants diminishes with decreasing soil moisture. Moisture movement from deep roots in moist soils to shallow roots in dry soils could make shallow soil nutrients available through the process of hydraulic lift (Passioura, 1988; Caldwell and Richards, 1989; Caldwell et al., 1991). Mycorrhizae could play a role in this process (Richards and Caldwell, 1987; Caldwell et al., 1991).

Plant species vary in their dependency on the fungal

endophytes. Plant species are defined as to their mycorrhizal dependence: Non-mycotrophs, facultative mycotrophs, and obligate mycotrophs (Janos, 1980). Many non-mycotrophs are ruderal pioneers of harsh sites. Facultative mycotrophs are susceptible to infection, but may not require it, especially in relatively fertile environments. Some grasses, including cheatgrass (Bromus tectorum), may be independent of mycorrhizae. Obligate mycotrophs are those plants which would rarely occur in nature without fungal endophytes and are dependent on mycorrhizae to establish and survive. Many of the shrubs species native to the Columbia Basin assessment area are obligate mycotrophs and require VA inoculum.

Seedling recruitment and the diversity of species declines when VAM fungi are absent from an area. This is particularly seen during secondary succession (Grime et al., 1987, Gange et al., 1990) Mosse et al. (1981) stated that the early establishment phase for a plant may be the stage in its life cycle when it is most dependent upon the fungal symbiont.

In summary, VAM fungi have been shown to be of particular benefit to their host plants in nutrient poor soils and extreme environments. It has been demonstrated that the symbiosis can have the impact of improving the plants ability to grow in stressed environments (Molina et al.,1978; Miller, 1979; Bethlenfalvay et al., 1984; Allen and Allen, 1986). In stressful environments, mycorrhizal species are likely to enjoy a

competitive advantage over nonmycorrhizal species (Doerr et al., 1984; Fitter, 1985).

# SPECIES OF SPECIAL CONCERN

A large number of plant species characteristic of sage-brush steppe habitat in the Columbia Basin assessment have been studied to determine their mycorrhizal status. The species lists indicate a large proportion of those plants are mycotrophic and, in many cases, obligately mycotrophic. Of particular importance, is the fact that dominant shrub species and native bunchgrassess are mycorrhizal. In contrast to the status of our knowledge on the plant host species, we have relatively little knowledge of the mycorrhizal fungal associates. Relatively few studies have documented specifically the VAM fungi for their study sites, and hence, we have little knowledge of the true diversity of VAM fungi in this habitat. Further, little is known about possible ecotypic adaptations and the range of soil and host preferences of these species.

Until more information is available on VAM fungal species for specific sites and for individual plant species, it is not possible to select fungal species of special concern. Rather, it is more appropriate to discuss the elements of the plant communities that are of special concern in the preservation of the mycorrhizal association and mycorrhizal propagules (hyphae and/or spores). Shrub species are one of the important components in rangeland systems for initial establishment and, ultimately, maintenance of VAM species. Goodwin (1992) documents the importance of shrubs in the establishment and recovery of VAM

fungi populations in soils, and, further, discusses the colonization of bunchgrasses by VAM as it relates to their In the Intermountain competitive abilities in rangeland systems. West, the native bunchgrasses are mycorrhizal, yet alien weeds (e.g. Bromus tectorum L.) introduced into disturbed sagebrush steppe habitat will often be nonmycorrhizal. When nonmycorrhizal species of plants establish in disturbed rangeland sites, the VAM fungal population will decline. In the absence of VAM fungi, native plants which are normally colonized by VAM fungi have a difficult time establishing due to lack of a symbiont. the native plants will be at a competitive disadvantage in capturing limited soil resources as compared to nonmycorrhizal alien species. However, if the native mycorrhizal species of plants are colonized by fungi, then they will out-compete the nonmycorrhizal plant species.

Although the amount of information on species of VAM associated with specific host plants is limited for the Columbia Basin assessment, 'that which is available indicates that there is some degree of host and site specificity. For example, a review of Tables 1 and 2 shows that the VAM fungal populations associated with the more volcanic soils in Central Oregon were different than the populations of VAM fungi associated with the lower elevation, drier sites. However, none of these studies indicate specificity of VAM mycorrhizal fungus with any one species of plant, and it would seem that most VAM fungi can form mycorrhizae with a diversity of plants. Hence, it appears that

the populations of VAM fungal species at a site can be considered as "pooled inoculum". It also appears that shifts in the composition of the vegetation (i.e. disturbance due to fire, grazing, mining, motor vehicles, etc.) will cause an accompanying shift in the VAM fungal composition, quantitatively and qualitatively...

#### MANAGEMENT OF DISTURBED LAND WITH RESPECT TO MYCORRHIZAE

In a mycorrhizal association with plants, the fungus is considered as the obligate symbiont, and, hence, any disturbance affecting the plant will result in a fungal response (Skujins and Allen, 1986). In arid and semi-arid regions of western North America, this relationship between mycorrhizae and land disturbance was initially noted during studies of revegetation of surface mines and mine spoils (Christensen and Williams, 1977; Stahl et al., 1979; Allen and Allen, 1980; Call and McKell, 1981; Loree and Williams, 1981; Loree and Williams, 1984; Danielson, 1985). These initial studies, and subsequently others, have shown that only about 1% of colonizing plants on a disturbed site are mycorrhizal, whereas on the adjacent, undisturbed sites about 99% are mycorrhizal. Studies have shown that most successful pioneers of disturbed sites and new soils are non-mycorrhizal plants, and that many plants may require VA mycorrhizal infection in order to colonize disturbed lands (Miller, 1979; Reeves et al., 1979).

Disturbance of arid lands significantly reduces the inoculum potential of the soil (i.e. propagules and/or stability of hyphal network) (Reeves et al., 1979). Plants that do not require mycorrhizal infection will be successful on disturbed sites.

Non-mycotrophic weeds, such as <u>Salsola kali</u> and <u>Haloseton</u>

<u>slomeratus</u> can invade disturbed sites rapidly and compete with desired grasses and forbs for water and nutrients. Since many of

the invading weed species are non-mycorrhizal,. without host plants' the VAM fungal propagules in the soil may not be able to persist. Disturbed sites, invaded by and subsequently dominated with weeds, have reported no VAM for up to 10 years. The persistence of communities of these plants will fail to support mycorrhizal populations and thus influence succession of disturbed ecosystems (Allen and Allen, 1980).

Various types of disturbances can occur in semi-arid grasslands. Examples of some disturbance types include: mining, overgrazing, cultivation, fire, vehicle use, etc. Land disturbance will have the following impact on mycorrhizae:

1) lowers mycorrhizal inoculum potential (disturbance of hyphal network and fewer propagules); 2) creates a nutrient pulse available to plants; 3) in early successional stages of recolonization, nonmycorrhizal species will dominate; 4) success of non-mycorrhizal species further reduces the propagules of mycorrhizal fungi; 5) succession is slowed because of the lack of potential mycorrhizal fungi.

Following disturbance, the processes involved with the restoration of desirable vegetation must also involve the restoration of the mycorrhizal association. The critical phases in restoration of the association are: 1) survival of residuals (spores and mycelial network), 2) migration of plant and fungal propagules to a location wherein contact can be made, and 3) the environmental characteristics in which establishment occurs.

Restoration of disturbed lands has prompted a greater understanding of recovery of mycorrhizae into the ecosystem.

Methods used in the re-establishment of VAM in order to promote recovery of desired plant communities are land management, inoculation, and natural processes.

# 1). Land Management

In situations where land is to be disturbed and degradation has not yet occurred, proper land management can be an effective means to preserve VAM and restore desirable plants. Retention of soil organic matter will maintain a soil nutrient supply and will help to promote establishment and persistence of VAM.

Maintenance of a continuous vegetational cover will allow a supply of carbon for fungal survival. Cultivation of land reduces VAM fungal densities and alters their species diversity (Skujins and Allen, 1986). Tilling of soil will disrupt hyphal networks and causes VAM spores to decompose more rapidly. The use of minimum tillage (no-till) will aid in the maintenance of VAM in the soil. Additionally, inorganic fertilizers, especially superphosphate, should be used with care, since they can drastically inhibit VAM formation.

One of the most successful land management methods has been used following disturbance due to mining. The retention and respreading of topsoil has been used to reestablish VAM and the desirable plant species.. Allen and Allen (1980) reported that infection frequency and spore counts were recovered to within 50%

of undisturbed sites in 3 years after topsoil was re-spread on disturbed sites. Whereas, in a site where topsoil was not retained, no infection was observed and non-VAM weeds still predominated 10 years after reclamation efforts began. Even the addition of relatively small amounts of fresh topsoil (2-4 cm in depth) to a site resulted in improved infectivity (Danielson et al., 1979; Zak and Parkinson, 1981).

# 2.Inoculation

Efforts to use VAM fungal inoculum additions to soil and/or VAM inoculated plants in outplantings at disturbed areas have had limited success. Lack of techniques for mass production of inocula, introduction of the correct fungal species into the appropriate habitats, and expenses involved with the production and inoculation procedures have limited the effectiveness and use of VAM inoculations.

# 3.Natural Succession

Recent studies have encouraged the use of natural successional processes to promote the dispersal and establishment of VAM. In arid soils; shrubs establish themselves in patches or clumps and form "fertile islands". These islands are also sites of highest VAM activity. In disturbed areas, the development of patches composed of shrubs and grasses should be planted. These patches will be inoculum focal points from which vegetation and VAM can spread. With greater shrub establishment, adequate VAM inoculum will be concentrated to initiate mycorrhizae on later

successional desirable plants (Allen, 1987).

Rehabilitation of disturbed sites should include techniques designed to stimulate re-establishment of VAM symbiosis.

#### RESEARCH RECOMMENDATIONS

Vesicualar-arbuscular mycorrhizal fungi are essential components of natural semi-arid land plant communities. Many questions remain unanswered on VAM in the Columbia Basin assessment, and additional research is needed. Future research should focus on the roles of mycorrhizal fungi in establishment and relative competitive abilities -of the important native shrub and bunchgrass as compared to the alien grasses. In order to accomplish this, more knowledge is needed on the plant species and their specific fungal symbionts. Further, it will be essential to determine for individual species of VAM if there are ecotypic adaptations and what is the range of soil and host preferences.

# LITERATURE CITED

- Allen, E.B. and Allen, M.F. 1980. Natural re-establishment of vesicular-arbuscular mycorrhizae following strip-mine reclamation in Wyoming. Journal of Applied Ecology, 17:139-147.
- Allen, E.B. and M.F. Allen. 1986. Water relations of xeric grasses in the field: interactions of mycorrhizas and competition. New Phytol. 104: 559-571.
- Allen, M.F. 1987. Ecology of vesicular-arbuscular mycorrhizae in an arid ecosystem: Use of natural processes promoting dispersal and establishment. In: Proceedings of the 7th North American Conference on Mycorrhizae, eds. Sylvia, D.M., L.L. Hung, and J.H. Graham. pp. 133-135. Gainesville, Florida: University of Florida.
- Allen, M.F. 1988. Belowground spatial patterning: influence of root architecture, microorganisms, and nutrients on plant survival in arid lands. In The Reconstruction of Disturbed Arid Lands: an Ecological Approach, ed. E.B. Allen, pp. 113-135. Westview Press, Boulder, CO.
- Allen, M.F. 1991. The ecology of mycorrhizae. Cambridge University Press, Cambridge. pps. 184.

- Allen, M.F. and Boosalis, M.G. 1983. Effects of two species of VA mycorrhizal fungi on drought tolerance of winter wheat.

  New Phytologist, 93: 67-76.
- Bethlenfalvay, G.J., and SDakessian. 1984. Grazing effects on mycorrhizal colonization and floristic composition of the vegetation on a semiarid range in northern Nevada. J. Range Management 37(4): 312-316.
- Bethlenfalvay, G.J., R. Evans, and A. Lesperance. 1985.

  Mycorrhizal colonization of crested wheatgrass as influenced by grazing. Agronomy J. 77(2): 233-236.
- Blaisdell, J.P., R.B. Murray, and E.D. McArthur. 1982. Managing intermountain rangelands sagebrush-grass ranges. USDA Forest Service General Technical Report INT-134.

  Intermountain Forest and Range Experiment Station, Ogden, Utah.
- Barbour, M.B., J.H. Burk, and W.D. Pitts. 1987. Terrestrial Plant Ecology2nd ed. Benjamin/Cummings Publ. Co., Inc., Menlo Park, California. 634 p.
- Caldwell, M.M., and J.H. Richards. 1989. Hydraulic lift: water 'efflux from upper roots imploves effectiveness of water uptake by deep roots. Oecologia 79: 1-5.

- Caldwell, M.M., J.H. Richards, and W. Beyschlag. 1991. Hydraulic lift: ecological implications of water efflux from roots. In D. Atkinson, ed. Plant root growth: an ecological perspective. Blackwell Scientific Publications. pp. 423-436,.
- Call, C.A. and McKell, C.M. 1981. Effects of endomycorrhizae on establishment and growth of native plant species on processed oil shale spoils. Abstract in: Proceedings of the 34th Annual Meeting of the Society of Range Management.

  September, 1981. Calgary.
- Christensen, M. and Williams, S.E. 1977. Occurrence of vesicular-arbuscular mycorrhizae on shrubs and grasses in strip-mine regions of Wyoming. Abstract in: Proceedings of the Third North American Conference on Mycorrhizae. August, 1977. Atlanta.
- Danielson, R.M. 1985. Mycorrhizae and reclamation of stressed terrestrial environments. In: R.L. Tate, III and D.A. Klein (eds) Soil Reclamation Processes; Microbiological Analyses and Applications. Marcel Dekker, Inc. pp. 173-201.
- Danielson, R.M., J.Zak, and D. Parkinson. 1979. Plant growth and mycorrhizal development in amended coal spoil material.

  In: M.K. Wali (ed.) Ecology and Coal Resource Development.

  Pergamon Press, New York. pp. 912-919.

- Davidson, D.E. and Christensen, M. 1977. Root-microfungal and mycorrhizal associations in a shortgrass prairie.— In: The Belowground Ecosystem: A Synthesis of Plant-associated Processes, ed. J.K. Marshall, pp. 279-287. Colorado State University Press, Fort Collins, CO.
- Doerr, T.B., E.F. Redente, and F.B. Reeves. 1984. Effects of
   soil disturbance on plant succession and levels of
  mycorrhizal fungi in a sagebrush-grassland community. J.Range.
   ...
  Manage. 37: 135-139.
- Fitter, A.H. 1985. Functioning of vesicular-arbuscular mycorrhizas under field conditions. New Phytol. 99: 257-265.
- Friese, C.F. and Allen, M.F. 1988. The interaction of harvester ant activity. and VA mycorrhizal fungi. Proceedings of the Royal Society of Edinburgh, 94B: 176.
- Gerdemann, J.W. and Trappe, J.M. 1974 The Endogonaceae in the Pacific Northwest. Mycologia Memoir 5: 1-76.
- Goodwin, J. 1992. The role of mycorfhizal fungi in competitive interactions among native bunchgrasses and alien weeds: a

2

- review and synthesis. Northwest Science 66 (4): 251-260.
- Grime, J.P., J.M.L. Mackey, S.H. Hillier, and D.J. Read. 1987.

  Floristic diversity in a model system using experimental

  microcosms. Nature 328: 420-422.
- Gurr, J.E. and M.C. Wicklow-Howard. 1994. VA Mycorrhizal status of burned and unburned sagebrush habitat. In Monsen, S.B. and S.G. Kitchen. Proceedings Ecology and Management of Annual Rangelands. Report INT-GTR-313, USDA Forest Service, Intermountain Research Station, Ogden, UT. pp. 132-135.
- Ho, I., and J.M. Trappe. 1980. Vesicular-arbuscular mycorrhizae of halophtic grasses in the Alvord desert of Oregon. From:

  Trappe, J.M. 1981. Mycorrhizae and productivity of arid and semiarid rangelands. *In* J.T. Menassah and E.J. Briskey (eds)

  Advances in Food Producing Systems for Arid and Semiarid

  Lands. Academic Press. New York. Pp. 581-589.
- Janos, D.P. 1980. Mycorrhizae influence tropical succession.
  Biotropica 12: 56-64.
- Laiho, 0. 1965. Further studies on the ectendotrophic mycorrhizae. Acta Forestalia Fennica 79:35.
- Lindsey, D.L. 1984. The role of vesicular-arbuscular mycorrhizae in shrub establishment. In Williams, S.E. and M.F. Allen.

- 1984. VA Mycorrhizae and reclamation of arid and semi-arid lands. Wyoming Agricultural Experiment Station, University of Wyoming, Laramie, WY., Scientific Report SA1261. Pp.53-68.
- Loree, M.A.J. and Williams, S.E. 1981. Colonization of a revegetated surface mine by indigenous endomycorrhizal fungi.

  Abstract in: Proceedings of the Fifth North American Conference on Mycorrhizae. August, 1981. Quebec City.
- Loree, M.A.J. and Williams, S.E. 1984. Vesicular-arbuscular mycorrhizae and severe land disturbance. In: S.E. Williams and M.F. Allen (eds.) V.A. Mycorrhizae and Reclamation of Arid and Semi-arid Lands. Wyoming Agriculture Expt. Stn. Sci. Report No. SA1261. pp. 1-14.
- Marks, G.C. and Kozlowski, T.T., Eds. 1973. Ectomycorrhizae, their ecology and physiology. Academic Press, New York. pp. 444.
- Maser, C., Z. Maser, and R. Molina. 1988. Small-mammal mycophagy in rangelands of central and southeastern Oregon. J. Range Management 41(4): 309-312.
- Miller, R.M. 1979. Some occurrences of vesicular-arbuscular mycorrhiza in natural and disturbed ecosystems of the Red Desert. Canadian Journal of Botany 57: 619-623.

- Molina, R.J., J.M. Trappe, and G.S. Strickler. 1978.

  Mycorrhizal fungi associated with *Festuca* in the western

  United States and Canada. Can. 'J. Bot. 56:1691-1695.
- Mosse, B., D.P. Stribley, and F. LeTacon. 1981. Ecology of mycorrhizae and mycorrhizal fungi. Adv. Microb. Ecol. 5:137-210.
- Passioura, J.B. 1988. Water transport in and to roots. Annual review. Plant Physiologist 39: 245-265.
- Read, D.J. 1984. The structure and function of the vegetative mycelium of mycorrhizal roots. In: The Ecology and Physiology of the Fungal Mycelium, ed. D.H. Jennings and A.D.M. Rayner, pp. 215-240. Cambridge University Press, Cambridge.
- Read, D.J., Francis, R. and Finlay, R.D. 1985. Mycorrhizal mycelia and nutrient cycling in plant communities. In:

  Ecological Interactions in Soil, ed. A.H. Fitter, pp. 193-217. Blackwell Scientific Publications, Oxford.
- Reeves, F.B., Wagner, D., Moor-man, T., and Kiel, J. 1979. The role of endomycorrhizae in revegetation practices in the semi-arid west. I. A comparison of incidence of mycorrhizae

- in severely disturbed vs. natural environments. American Journal of Botany 66: 6-13.
- Rose, S.L. 1980. Mycorrhizal associations of some actinomycete nodulated nitrogen-fixing plants. Can. J. Bot. 58: 1449-1454.
- Rose, S., B.A. Daniels, and J.M. Trappe. 1979. *Glomus Gerdemannii* sp.nov. Mycotaxon 8: 297-301.
- Rose, S.L., J.M. Trappe. 1980. Three new endomycorrhizal *Glomus*spp. associated with actinorrhizal shrubs. Mycotaxon 10: 413-420.
- Safir, G.R. and Nelsen, C.E. 1985. VA mycorrhizas: plant and fungal water relations. In: Proceedings of the 6th North

  American Conference on Mycorrhizae, ed. Molina, R. pp. 161164. Corvallis, Oregon: Oregon State University.
- Skujins, J. and Allen, M.F. 1986. Use of mycorrhizae for land rehabilitation,. MIRCEN Journal, 2: 161-176.
- Stahl, P.D., Allen, M.F., Allen, E.B. and Christensen, M. 1979.

  Occurrence of vesicular-arbuscular mycorrhizal propagules in disturbed and undisturbed sites in Wyoming. Abstract in:

  Proceedings of the Fourth North American Conference on Mycorrhizae. August, 19.79.

- Trappe, J.M. 1962. Fungus associates of ectotrophic mycorrhizae. Botanical Review 28: 538-606.
- Trappe, J.M. 1981. Mycorrhizae and productivity of arid and semi-arid rangelands. In: Advances in Food Producing Systems for Arid and Semi-arid Lands, ed. J.T. Manassah and E.J. Briskey, pp. 581-599. Academic Press, New York.
- Trent, J.D., T.J. Svejcar, and R.R. Blank. 1994. Mycorrhizal colonization, hyphal lengths, and soil moisture associated with two Artemisis tridentata subspecies. Great Basin Naturalist 54 (4): 291-300.
- Warner, N.J., Allen, M.F. and MacMahon, J.A. 1987. Dispersal agents of vesicular-arbuscular mycorrhizal fungi in a disturbed arid ecosystem. Mycologia 79: 721-730.
- West, N.E. 1988. Intermountain deserts, shrub steppes, and woodlands. Pages 210-230 in M. G. Barbour and W. D. Billings, eds. North American terrestrial vegetation.

  Cambridge University Press, Cambridge.
- West; N.E. 1991. Nutrient cycling in soils of semiarid and arid regions. In J. Skujins, ed., Semiarid lands and deserts: soil resources and reclamation. Marcel Dekker Inc., New York, Basel, Hong Kong. pp. 295-332.

- Wicklow-Howard, M. 1982. The occurrence of vesicular-arbuscular mycorrhizae in disturbed and undisturbed ecosystems of the semi-'arid deserts of Idaho. Report of Boise State University Research Ctr. 14p.
- Wicklow-Howard, M. 1985. The occurrence of vesicular-arbuscular mycorrhiza associated with desert shrubs. Report of Boise State University Research Ctr. 7p.
- Wicklow-Howard, M. 1989. Th occurrence of vesicular-arbuscular mycorrhizae in burned areas of the Snake River Birds of Prey Area, Idaho. Mycotaxon 34:253-257.
- Zak, J. and Parkinson, D. 1981. Long term VA mycorrhizal development of slender wheatgrass in amended mine spoils.

  Abstract in: Proceedings of the Fifth North American Conference on Mycorrhizae. August, 1981. Quebec City.

APPENDIX A

TABLE 1. VESICULAR-ARBUSCULAR MYCORRHIZALSHRUBS FROM SAGEBRUSH-STEPPE HABITAT OF WESTERN IDAHO AND PARTS OF CENTRAL AND EASTERN OREGON

PLANT	COMMONNAME	SITE	VAM FUNGUS (IF KNOWN)
ASTERACEAE			
Artemisia spinescens	Budsage	Western Snake River Plains, ID	
Artemisia tridentata var. tridentata	Basin Big Sagebrush	Boise Front, ID	Glomus sp.
Artemisia tridentata var. wyomingensis	Wyoming Big Sagebrush	Western Snake River Plains, ID	Glomus microcarpus, Gigaspora sp.
Chrysothamnus nauseosus	Rabbitbrush	Boise Front, ID, Western Snake River Plains, ID	Glomus sp.
Gutierresia sarothrae	Broom Snakeweed	Western Snake River Plains, ID	
Tetradymia glabrata	Littleleaf Horsebrush	Western Snake River Plains, ID	
CHENOPODIACEAE			
Atripkx confertifofia	Shadscale	Western Snake River Plains, ID	
Atripkx nutallii	Nutall Saltbrush	Western Snake River Plains, ID	
Atripkx spinosa	Spiny Hopsage	Western Snake River Plains, ID	
Ceratoides lanata	Winterfat	Western Snake River Plains, ID	Glomus microcarpus
RHAMNACEAE			
Ceanothus velutinus	Snowbrush	Central Oregon	Gigaspora calospora, Glomus gerdemannii, Glomus Iacteus, Glomus halonatus
ROSACEAE			
Cercocarpus ledifolius		Central Oregon	Glomus scintillans
Purshia tridentata	Bitterbrush	Central Oregon	Gigaspara calospora, Glomus gerdemannii, Glomus lacteus, Glomus scintillans
P. tridentata		Boise Front, ID	Glomus sp.

VESICULAR-ARBUSCULAR MYCORRHIZAE OF PERENNIAL GRASSES AND FORBS FROM SAGEBRUSH STEPPE HABITAT IN WESTERN IDAHO AND PARTS OF EASTERN AND CENTRAL OREGON

PLANT	SITE	VAM FUNGUS (IF KNOWN)
ASTERACEAE		
Achillea millefolium	Boise Front, ID	
Balsamorhira sagitata	Boise Front, ID	
BORAGINACEAE		
Lithospermum ruderale	Boise Front, ID	
<u>LILIACEAE</u>		
Calochortus sp.	Boise Front, ID	
<u>POACEAE</u>		
Agropyron spicatum	Western Snake River Plains, ID	
Distichlis stricta	Harney Co., OR	
Festuca idahoensis	Western Snake River Plains, ID	
Festuca idahoensis	Hamey Co., OR	Glomus fasciculutus, G. tenuis, G. macrocarpus
Festuca idahoensis	Wallowa Co., OR	Glomus fasciculatus, G. tenuis, G. mosseae, G. microcarpus
Festuca ovina	Hamey Co., OR	Glomus fasciculatus, G. tenuis, G. microcarpus
Festuca scabrella	Hamey Co., OR	Glomus tenuis, G. microcarpus, Acaulospora laevis
Festuca scabrella	Wallowa Co., OR	Glomus fasciculatus
Festuca viridula	Wallowa Co., OR	Glomus fasciculatus, G. tenuis, G. macrocarpus var. macrocarpus, Gigaspora calospora, Acaulospora laevis
Festuca viridula	Union Co., OR	Glomus fasciculatus, Gigaspora calospora, Acaulospora laevis, Acaulospora scrobiculota
Festuca viridula	Columbia Co., WA	Glomus fasciculatus, G. tenuis, G. macrocarpus var. macrocarpus, Gigaspora calospora, Acaulospora scrobiculata

PLANT	SITE	VAM FUNGUS (IF <b>KNOWN)</b>
Poo snndbrcrgii	Western Snake River Plains, ID	
Sitanion hystrix	Western Snake River Plains, ID	
Stipa comata	Weskrn Snake River Plains, ID	
Stipa thurberiana	Western Snake River Plains, ID	
POLEMONIACEAE  Phlox sp.	Boise Front, ID	
<i>гтох</i> вр.	Boise Profit, ID	
ROSACEAE  Rosa woodsii	Boise Front, ID	
SAXIFRAGACEAE  Lithophragma bulbifera	Boise <b>Front,</b> ID	
UMBELLIFERAE  Lomatium triternatum	Boise Front, ID	
VIOLACEAE		
Viola purpurea	Boise Front, ID	